

Comparative osteology of the suspensorial and opercular series in representatives of the eurypterygian fishes

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Abstract: The osteology of the suspensorial and opercular series in representatives of 49 genera and 41 families of eurypterygian fishes were studied. The suspensorium consists of the palatine, ectopterygoid, endopterygoid, metapterygoid, quadrate, symplectic, and hyomandibular bones. The hyomandibular foramen is present at the base of the anterior head. The opercular series consists of the preopercle, subopercle, interopercle, and opercle. In most Eurypterygii, the preopercle is L-shaped and bears an open or closed preoperculomandibular canal.

Keywords: Bone, Eurypterygii, Opercula, Osteology, Suspensorium.

Introduction

Eurypterygian fishes composed of several orders including Aulopiformes, Myctophiformes, Lampridiformes, Polymixiiformes, Percopsiformes, Mugiliformes, Atheriniformes, Beloniformes, Cyprinodontiformes, Stephanoberyciformes, Beryciformes, Zeiformes, Gasterosteiformes, Synbranchiformes, Scorpaeniformes, Perciformes, Pleuronectiformes and Tetraodontiformes (Nelson 2006). Despite the introduction of modern techniques, osteological features still play an important role in the systematic and biological studies of fishes (e.g., Britz & Conway 2009; Keivany & Nelson 2006; Nasri et al. 2013; Keivany 2014; Eagderi & Adriaens 2014; Ghanbarzadeh et al. 2014). Therefore, this study was aimed to describe the diversity of suspensorial and opercular skeletons of eurypterygian fishes. The present study describes and illustrates the variables and significant features of the suspensorial and opercular series of the eurypterygians at higher level with selected taxa from each order in separate sections. The systematic of the taxa follows Nelson (2006).

Materials and methods

The selected specimens (see below) were cleared and

stained according to Taylor and Van Dyke's (1985) protocol. A Camera Lucida attached to a Wild M5 dissecting microscope was used for examination of specimens and drawings. The bones in the first figure of each anatomical section are arbitrarily shaded and labeled and in the others, they are shaded in a consistent manner (dark, medium, and clear) to facilitate comparison among the taxa. Forty nine genera representing 41 families were studied. Most of the specimens were obtained from the University of Alberta Museum of Zoology (UAMZ). Some were obtained from the Smithsonian Institution (United States National Museum) (USNM), California Academy of Sciences (CAS), and Australian Museum at Sydney (AMS). Numbers in parentheses indicate the standard length in millimeters of specimens; those in bold are specimens used for figuring osteology of the taxa. The number of genera studied in each order is: Aulopiformes (1), Myctophiformes (1), Lampridiformes (2), Polymixiiformes (1), Percopsiformes (1), Mugiliformes (1), Atheriniformes (2), Beloniformes (2), Cyprinodontiformes (2), Stephanoberyciformes (2), Beryciformes (2), Zeiformes (2), Gasterosteiformes (18) Synbranchiformes (2), Scorpaeniformes (including Dactylopteridae) (5),

and Perciformes (including Elasmobranchii) (5).

Aulopiformes

Synodontidae (lizardfishes)

Synodus synodus UAMZ 1806 (147).

Synodus intermedius UAMZ 4889 (78).

Myctophiformes

Myctophidae (lanternfishes)

Myctophum sp. UAMZ 2689 (60, 77, 80).

Lampridiformes

Veliferidae

Velifer hypselopterus AMS 21839005 (101, 115).

Trachipteridae (ribbonfishes)

Trachipterus altivelis CAS 24297 (85), CAS 51177 (105).

Polymixiiformes

Polymixiidae (beardfishes)

Polymixia lowei USNM 159300 (81, 115).

Percopsiformes

Percopsidae (trout-perches)

Percopsis omiscomaycus UAMZ 2048 (17, 19, 27, 55, 60).

Mugiliformes

Mugilidae (mullets)

Mugil sp. UAMZ 5125 (55, 63, 63, 66, 91).

Atheriniformes

Melanotaeniidae (rainbowfishes)

Melanotaenia sp. UAMZ 3526 (40, 42, 51).

Atherinidae (silversides)

Allanetta harringtonensis UAMZ 2673 (47, 58, 59, 60, 61).

Beloniformes

Belonidae (needlefishes)

Pseudotylotus sp. UAMZ 8165 (173).

Hemiramphidae (halfbeaks)

Arrhamphus sclerolepis UAMZ 3523 (103).

Cyprinodontiformes

Aplocheilidae (rivulines)

Rivulus hartii UAMZ 6660 (44, 47).

Cyprinodontidae (pupfishes)

Cyprinodon nevadensis UAMZ 3114 (24, 34, 41).

Stephanoberyciformes

Stephanoberycidae (pricklefishes)

Stephanoberyx monae USNM 304353 (85, 92).

Rondeletidae (redmouth whalefishes)

Rondeletia loricata AMS 21141001 (88), AMS 20523001 (34, 37), AMS 18813001 (53).

Beryciformes

Monocentridae (pinecone fishes)

Monocentris sp. UAMZ 7854 (92).

Holocentridae (squirrelfishes)

Sargocentron vexillarium UAMZ 5075 (34, 34, 40, 44, 84).

Zeiformes

Grammicolepididae

Xenolepidichthys dalgleishi USNM 322673 (68, 75).

Caproidae (boarfishes)

Antigonia sp. USNM 266901 (37, 41).

Gasterosteiformes

Hypoptychidae (sand eel)

Hypoptychus dybowskii UAMZ 5550 (75, 80, 81).

Aulorhynchidae (tubesnouts)

Aulorhynchus flavidus UAMZ 3783 (104, 105, 109).

Aulichthys japonicus UAMZ 5542 (47, 48).

Gasterosteidae (sticklebacks)

Spinachia UAMZ 6582 (25, 53, 55).

Apeltes quadracus UAMZ 7958 (34, 37, 39).

Gasterosteus aculeatus UAMZ 3894 (32, 57, 58, 58, 73, 77, 83).

Culaea inconstans UAMZ 3797 (21, 30, 49, 56, 57, 58, 60).

Pungitius UAMZ 3049 (39, 43, 46, 55).

Pegasidae (seamoths)

Pegasus volans UAMZ 4616 (99, 104).

Solenostomidae (ghost pipefishes)

Solenostomus paradoxus AMS 17111002 (51), AMS 17160002 (50), AMS 18852002 (52), AMS 18314001 (59).

Syngnathidae (pipefishes and seahorses)

Syngnathus scovelli UAMZ 3782 (117).

Syngnathus griseolineatus UAMZ 3469 (225, 240, 272).

Hippocampus ingens UAMZ 3594 (170).

Indostomidae (nailfishes)

Indostomus paradoxus UAMZ 6700, CAS 64017 (23, 23, 24, 25).

Aulostomidae (trumpetfishes)

Aulostomus valentini CAS 11979 (139).

Aulostomus sp. CAS 145550 (109, 125).

Aulostomus maculatus CAS 145176 (213), CAS 145549 (171).

Fistulariidae (cornetfishes)

Fistularia petimba UAMZ 6348 (125, 158, 171).

Macroramphosidae (snipefishes)

Macroramphosus scolopax USNM 344398 (94, 99, 99, 100).

Centriscidae (shrimpfishes)

Centriscus scutatus UAMZ 3480 (94, 107).

Aeoliscus strigatus UAMZ 4048 (79, 89).

Synbranchiformes

Synbranchidae (swamp-eels)

Monopterus albus USNM 192939 (193, 245).

Mastacembelidae (spiny eels)

Macrognathus aculeatus UAMZ 1625 (120), UAMZ 1855 (119).

Scorpaeniformes

Dactylopteridae (flying gurnards)

Dactylopterus volitans UAMZ 2633 (61, 74).

Dactyloptena sp. UAMZ 7519 (65).

Scorpaenidae (rockfishes)

Sebastes caurinus UAMZ 3142 (71, 75).

Hexagrammidae (greenling)

Hexagrammos decagrammus UAMZ 3190 (47, 50).

Agonidae (poachers)

Xeneretmus latifrons UAMZ 3196 (90, 95, 143).

Perciformes

Percidae (perches)

Perca flavescens UAMZ 1244 (50, 51, 52, 54, 55).

Cirrhitidae (hawkfishes)

Amblycirrhitis pinos UAMZ 3640 (24, 25, 26, 45, 61).

Elassomatidae (pygmy sunfishes)

Elassoma zonatum UAMZ 6920 (26, 29, 30).

Pomacentridae (damselfishes)

Stegastes partitus UAMZ 3640 (12, 12, 13, 14, 25, 34, 47).

Centrarchidae (sunfishes)

Lepomis gibbosus UAMZ 7715.4 (23, 24, 25, 31, 40).

Results and Discussion

The suspensorium is comprised of the palatine, ectopterygoid, endopterygoid, metapterygoid, quadrate, symplectic, and hyomandibular. The hyomandibular has three articular condyles (heads) including two on its dorsal edge and another one on its posterior rim. The anterior condyle articulates with the sphenotic, the middle one with the pterotic, and the posterior condyle with the opercle. The hyomandibular foramen is present at the base of the anterior head.

The opercular series consists of the preopercle, subopercle, interopercle, and opercle. In most Eurypterygii, the preopercle is L-shaped and bears an open or closed preoperculomandibular canal. Skeletal terminology follows Rojo (1991) for the suspensorium and opercular series, but use of "ventral process" of the quadrate for the quadratojugal process.

Aulopiformes

Synodontidae (Fig. 1). The palatine is long, compressed, toothed, and with a medial cylindrical head. The ectopterygoid is L-shaped, autogenous and its posteroventral arm lies anterior to the quadrate anterior arm. The endopterygoid is narrow and connected to the medial surface of the palatine. The

metapterygoid is large, triangular and autogenous. The quadrate is U-shaped, with ascending anterior and posterior arms, and a ventral process. The symplectic is short, rod-like, and fully inserted in the quadrate posterior arm. The hyomandibular bears distinct dorsal condyles and intercondyle, anterior and posterior flanges.

The preopercle is smooth, its ventral arm is indistinct, and bears a preoperculomandibular canal. The interopercle is triangular, large, and overlaps the subopercle. The subopercle bears a small anterior ascending process and its posterior margin is round. The subopercle is the largest element and covers most of the gill opening. The opercle is small and roughly square. In *Bathysaurus*, the quadrate is fan-like, but the symplectic is small and fully inserted in the quadrate (Baldwin & Johnson 1996). In *Pseudotrichonotidae*, the quadrate is fan-like, the symplectic is large and not fully inserted in the quadrate, the ventral arm of preopercle is distinct, the opercle is triangular, and the interopercle is elongated (Johnson et al. 1996).

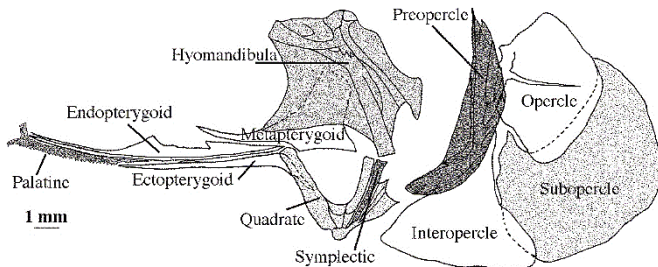


Fig.1. Lateral view of the suspensorium and opercular series in *Synodus intermedius* (Synodontidae) (UAMZ 4889, 78 mm).

Myctophiformes

Myctophidae. The palatine is long, bears a laterally projected head with numerous tiny teeth, and is tightly connected to the ectopterygoid. The ectopterygoid is T-shaped, autogenous, and its posterodorsal arm overlies the quadrate medial surface. The endopterygoid is broad and connected to the medial surface of the ectopterygoid. The metapterygoid is large and autogenous. The quadrate is fan-like and with a distinct ventral process. The symplectic is short, rod-like, and fully inserted in the

quadrate. The hyomandibular bears distinct dorsal condyles and intercondyle and anterior flanges.

The preopercle is smooth, its ventral arm is indistinct, and bears a preoperculomandibular canal and a thin broad posterior flange. The interopercle is triangular and large and overlaps the subopercle. The subopercle lacks a distinct anterior ascending process and its posterior margin is blunt. The opercle is roughly square and bears a dorsal strut.

Lampridiformes

Veliferidae (Fig. 2). The palatine is short, cylindrical, edentulous, with a laterally projected and bifurcated head, and abuts the ectopterygoid posteriorly. The ectopterygoid is slightly curved and autogenous. The endopterygoid is broad and connected to the medial surface of the ectopterygoid. The metapterygoid is large and autogenous. The quadrate is fanlike and with a ventral process. The symplectic is short, rod-like, and fully inserted in the quadrate. The hyomandibular is long and lacks distinct dorsal condyles, but bears a lateral lamina and a small anterior flange. In *Metavelifer*, the palatine and ectopterygoid are broad and the hyomandibular bears a distinct posterodorsal condyle (Olney et al. 1993). The preopercle is smooth, with a distinct short ventral

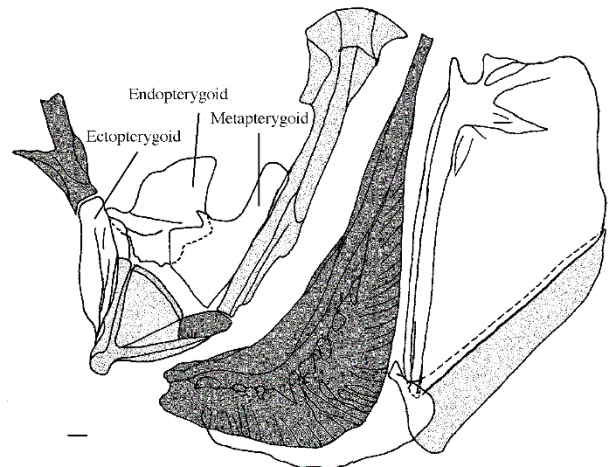


Fig.2. Lateral view of the suspensorium and opercular series in *Velifer hypselopterus* (Veliferidae) (AMS 21839005, 101 mm).

arm, and bears a preoperculomandibular canal. The interopercle is roughly ovoid and overlaps the

subopercle. The subopercle bears a distinct ascending process and its posterior margin is pointed. The opercle bears an anterior strut.

Polymixiiformes

Polymixiidae (Fig. 3). The palatine is short, with tiny teeth, and a laterally projected cylindrical head. The ectopterygoid is L-shaped and autogenous. The endopterygoid is broad and connected to the medial surface of the palatine and ectopterygoid. The metapterygoid is large and autogenous. The quadrate is fanlike and without a distinct ventral process. The symplectic is short, rod-like, and fully inserted in the quadrate. The hyomandibular is long and bears distinct dorsal condyles, a lateral lamina, and intercondyle and anterior flanges.

The preopercle is toothed, without a distinct ventral arm, and bears a preoperculomandibular canal. The interopercle is roughly ovoid and abuts the subopercle posteriorly. The subopercle bears a distinct ascending process and its posterior margin is blunt. The opercle bears the anterior and dorsal struts.

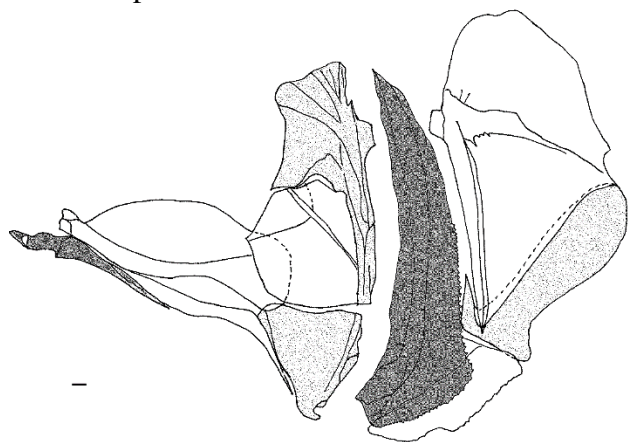


Fig.3. Lateral view of the suspensorium and opercular series in *Polymixia lowei* (Polymixiidae) (USNM 159300, 115 mm).

Percopsiformes

Percopsidae (Fig. 4). The palatine is short, edentulous, and with a laterally projected cylindrical head. The ectopterygoid is slightly curved and autogenous. The endopterygoid is broad and connected to the medial face of the ectopterygoid.

The metapterygoid is large and autogenous. The quadrate is fan-like and with a highly expanded ventral process. The symplectic is long, rod-like, with dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular bears a distinct posterior dorsal condyle, a lateral lamina, and an anterior flange.

The preopercle is toothed, with a distinct long ventral arm, and bears a preoperculomandibular canal. The interopercle is long, broad, and abuts the subopercle posteriorly. The subopercle bears a distinct ascending process and its posterior margin is pointed. The opercle bears the anterior and dorsal struts.

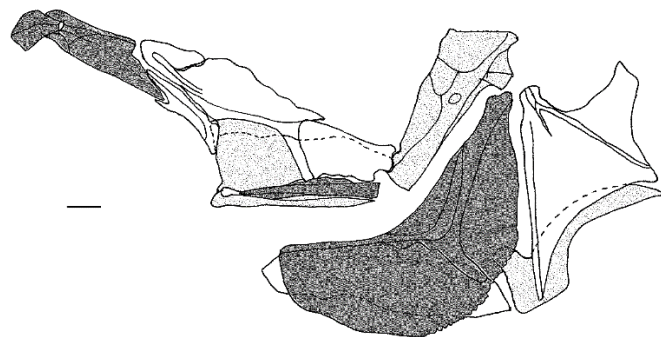


Fig.4. Lateral view of the suspensorium and opercular series in *Percopsis omiscomaycus* (Percopsidae) (UAMZ 2048, 55 mm).

Mugiliformes

Mugilidae. The palatine is short, toothed, and with a small laterally projected cylindrical head. The ectopterygoid is slightly curved and autogenous. The endopterygoid is broad and connected to the medial surface of the palatine and ectopterygoid. The metapterygoid is large and autogenous. The quadrate is fanlike and with a long ventral process. The symplectic is long, rod-like, with small dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange.

The preopercle is smooth, with a distinct long ventral arm, and bears a preoperculomandibular canal. The interopercle is triangular, long, and slightly overlaps the subopercle posteriorly. The subopercle bears a distinct ascending process and its

posterior margin is pointed. The opercle bears an anterior strut.

Atheriniformes

Melanotaeniidae. The palatine is short, toothed, with a laterally projected cylindrical head, and lies on the lateral surface of the ectopterygoid. The ectopterygoid is slightly curved. The endopterygoid is broad with a lateral wing that articulating with the quadrate. The metapterygoid is large and overlies the symplectic and hyomandibular. The quadrate is fanlike, with a distinct ventral process. The symplectic is long, rod-like, with small dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular bears a distinct posterodorsal condyle, a lateral lamina and an anterior flange.

The preopercle is smooth, with a distinct long ventral arm, and bears a preoperculomandibular canal. The interopercle is triangular, long, and slightly overlaps the subopercle posteriorly. The subopercle bears a distinct ascending process and its posterior margin is pointed. The opercle lacks an anterior strut.

Atherinidae (Fig. 5). The palatine is short, edentulous, with a laterally projected cylindrical head, and lies on the lateral surface of the ectopterygoid. The ectopterygoid is slightly curved. The endopterygoid is broad with a lateral wing that articulating with the quadrate. The metapterygoid is large and overlies the symplectic and hyomandibular. The quadrate is fan-like and with a distinct ventral process. The symplectic is long, rod-like, with small dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular bears distinct dorsal condyles, a small lateral lamina, and an anterior flange.

The preopercle is smooth, with a distinct long ventral arm, and bears a preoperculomandibular canal. The interopercle is triangular, long, and slightly overlaps the subopercle posteriorly. The subopercle bears a distinct ascending process and its posterior margin is pointed. The opercle lacks struts. Also see Rosen & Parenti (1981).

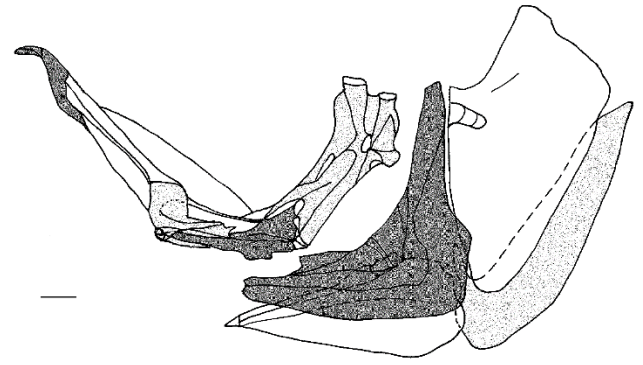


Fig.5. Lateral view of the suspensorium and opercular series in *Allanetta harringtonensis* (Atherinidae) (UAMZ 2673, 58 mm).

Beloniformes

Belonidae. The palatine is short, edentulous, without a distinct head, and tightly articulated with the ectopterygoid. The ectopterygoid is long, straight, and rod-like. The endopterygoid is narrow and connected to the medial face of the quadrate. The metapterygoid is large and overlies the symplectic and hyomandibular. The quadrate is fan-like, with a long anterior ascending process extending along the ectopterygoid and reaches the palatine, and bears a distinct ventral process. The symplectic is long, rod-like, with small dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange.

The preopercle is smooth, with a distinct long ventral arm, and bears a preoperculomandibular canal. The interopercle is long and slightly overlaps the subopercle posteriorly. The subopercle bears a distinct ascending process and its posterior margin is pointed. The opercle lacks an anterior strut.

Hemiramphidae (Fig. 6). The palatine is long, edentulous, with a laterally projected cylindrical head, and tightly articulated with the ectopterygoid and quadrate. The ectopterygoid is short, straight, and rod-like. The endopterygoid is broad and connected to the medial face of the quadrate. The metapterygoid is small and overlies the symplectic and hyomandibular. The quadrate is fan-like, with a long anterior ascending process that extends along the ectopterygoid and reaches the palatine, and bears

a distinct ventral process. The symplectic is well-developed, with expanded dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular bears a distinct posterodorsal condyle, a lateral lamina, and an anterior flange.

The preopercle is smooth, with a distinct long ventral arm, and bears a preoperculomandibular canal and a posteroventral process. The interopercle is broad and slightly overlaps the subopercle. The subopercle bears a distinct ascending process and a pointed posterior margin. The opercle lacks an anterior strut. Also see Rosen (1964).

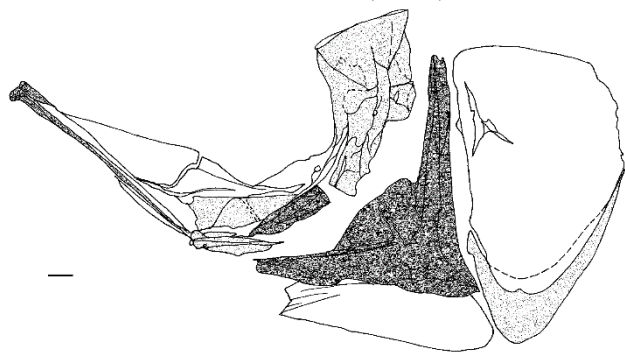


Fig.6. Lateral view of the suspensorium and opercular series in *Arrhamphus sclerolepis* (Hemiramphidae) (UAMZ 3523, 103 mm).

Cyprinodontiformes

Aplocheilidae (Fig. 7). The palatine is short, edentulous, with a laterally projected head, and articulated with the endopterygoid posteriorly. The ectopterygoid is not present as a distinct bone and may be fused to the palatine. The endopterygoid is expanded anteroventrally and lies over the quadrate. The metapterygoid overlies the symplectic and hyomandibular. The quadrate is fan-like and bears a long ventral process. The symplectic is well-developed, with expanded dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular bears dorsal condyles, a lateral lamina, and the intercondyle and anterior flanges.

The preopercle is smooth, with a broad ventral arm, and bears a preoperculomandibular canal. The interopercle is broad and slightly overlaps the subopercle posteriorly. The subopercle bears a

distinct ascending process and a pointed posterior margin. The opercle bears an anterior strut. Also see Rosen (1964) and Dyer & Chernoff (1996).

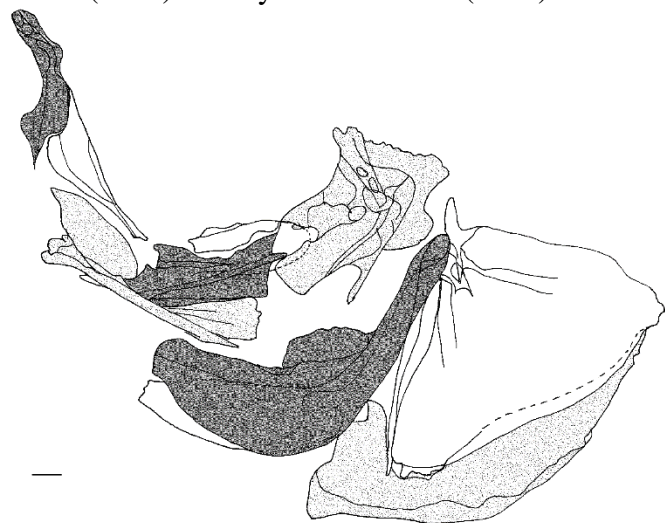


Fig.7. Lateral view of the suspensorium and opercular series in *Rivulus hartii* (Aplocheilidae) (UAMZ 6660, 47 mm).

Cyprinodontidae. The palatine is edentulous, with a small medially projected head, and articulated with the ectopterygoid and endopterygoid posteriorly. The ectopterygoid is curved and reduced. The endopterygoid overlies the quadrate. The metapterygoid is absent. The quadrate is fan-like and bears a large ventral process. The symplectic is well developed, with dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular bears dorsal condyles, a lateral lamina, and the intercondyle and anterior flanges.

The preopercle is smooth, with a broad ventral arm, and bears a preoperculomandibular canal. The interopercle is broad and slightly overlaps the subopercle posteriorly. The subopercle bears a distinct ascending process and a pointed posterior margin. The opercle bears an anterior strut. Also see Costa (1998), Rauchenberger (1989), Parenti (1981, 1984, 1993) and Keivany (2003).

Stephanoberyciformes

Stephanoberycidae (Fig. 8). The palatine is short, edentulous, with a cylindrical head, and articulated

with the ectopterygoid and endopterygoid posteriorly. The ectopterygoid is curved. The endopterygoid is broad. The metapterygoid is connected to the quadrate via cartilage. The quadrate is fan-like and bears a distinct ventral process. The symplectic is rod-like and mostly inserted in the quadrate. The hyomandibular bears a distinct posterodorsal condyle, a lateral lamina, and an anterior flange.

The preopercle is toothed, without a distinct ventral arm, and bears a preoperculomandibular canal. The interopercle is broad and short. The subopercle lacks a distinct ascending process and its posterior margin is blunt. The opercle is reduced and bears a strong anterior strut. Also see Kotlyar (1991a, b).

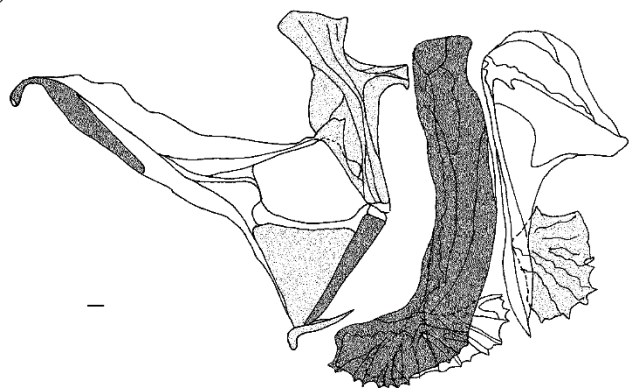


Fig.8. Lateral view of the suspensorium and opercular series in *Stephanoberyx monae* (Stephanoberycidae) (USNM 304353, 92 mm).

Rondeletiidae. The palatine is short, edentulous, with a laterally projected cylindrical head and a dorsomedial flange, and articulated with the ectopterygoid posteriorly. The ectopterygoid is L-shaped. The endopterygoid is absent. The metapterygoid is tightly connected to the hyomandibular and quadrate. The quadrate is fan-like and bears a distinct ventral process. The symplectic is hourglass shaped and mostly inserted in the quadrate. The hyomandibular bears distinct dorsal condyles, a lateral lamina, and an anterior flange. The posterodorsal condyle is enlarged.

The preopercle is smooth, with a distinct ventral arm and a posterior flange, and bears a

preoperculomandibular canal. The interopercle is highly reduced. The subopercle is triangular, lacks a distinct ascending process, and its posterior margin is pointed. The opercle bears anterior and dorsal struts.

Beryciformes

Monocentridae (Fig. 9). The palatine is short, with tiny teeth and a laterally projected head, and articulated with the ectopterygoid posteriorly. The ectopterygoid is curved. The endopterygoid is broad. The metapterygoid is connected to the quadrate. The quadrate is fan-like and bears a distinct ventral process. The symplectic is hourglass shaped and mostly inserted in the quadrate. The hyomandibular lacks distinct dorsal condyles, but bears a small lateral lamina and an anterior flange.

The preopercle bears two posteroventral spines, a short distinct ventral arm, and a preoperculomandibular canal. The interopercle is toothed ventrally. The subopercle is toothed, lacks a distinct ascending process, and its posterior margin is pointed. The opercle bears strong struts.



Fig.9. Lateral view of the suspensorium and opercular series in *Monocentris* sp. (Monocentridae) (UAMZ 7854, 92 mm).

Holocentridae. The palatine is short, toothed, with a laterally projected head, and articulated with the ectopterygoid posteriorly. The ectopterygoid is T-shaped, with a very small posterodorsal arm. The endopterygoid is broad. The metapterygoid is autogenous. The quadrate is fanlike and bears a

distinct ventral process. The symplectic is rod-like, with a small ventral flange, and not fully inserted in the quadrate. The hyomandibular bears a distinct posterodorsal condyle, a small lateral lamina, and a large anterior flange.

The preopercle bears several small spines and a strong posteroventral spine, a short ventral arm, and a preoperculomandibular canal. The interopercle is small. The subopercle bears a small ascending process and its posterior margin is blunt. The opercle bears an anterior strut, several small posterior spines, and two long spines. Also see Zehren (1979) and Kotlyar (1992).

Zeiformes

Grammicolepididae. The palatine is short, edentulous, with a straight cylindrical head, and is articulated with the ectopterygoid posteriorly. The ectopterygoid is curved posterodorsally covering the anterior and dorsal margins of the quadrate. The endopterygoid is broad. The metapterygoid is small and attached to the medial surface of the endopterygoid. The quadrate is fanlike and bears a distinct ventral process. The symplectic bears the dorsal and ventral flanges and is not fully inserted in the quadrate. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange.

The preopercle is toothed, with a distinct ventral arm, and bears a preoperculomandibular canal. The interopercle is broad. The subopercle bears a small ascending process and its posterior margin is pointed. The opercle bears an anterior strut.

Caproidae (Fig. 10). The palatine is short, edentulous, bears a laterally projected head, and articulated with the ectopterygoid and endopterygoid posteriorly. The ectopterygoid is triangular. The endopterygoid is broad. The metapterygoid bears a ventral process that via cartilage articulates with the symplectic-hyomandibular joint. The quadrate is fanlike and bears a distinct ventral process. The symplectic is simple and rod-like and not fully

inserted in the quadrate. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and a narrow anterior flange.

The preopercle is toothed, with a distinct ventral arm, angled distinctly, and bears a preoperculomandibular canal. The interopercle is long and broad posteriorly. The subopercle bears a small ascending process and its posterior margin is pointed. The opercle is reduced and bears an anterior strut. Also see Rosen (1984).

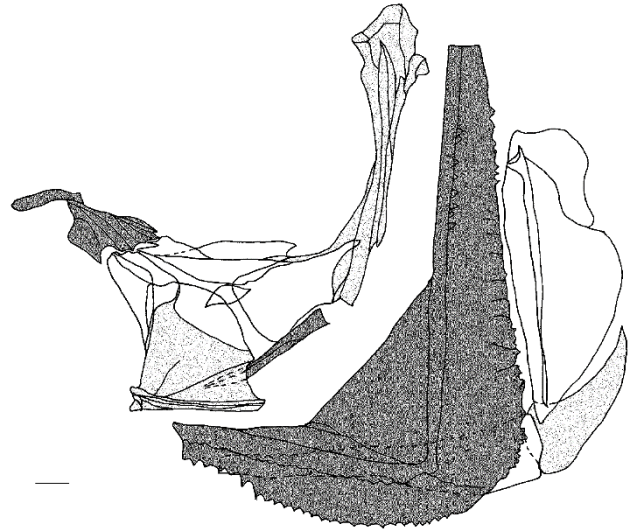


Fig.10. Lateral view of the suspensorium and opercular series in *Antigonia* sp. (Caproidae) (USNM 266901, 37 mm).

Gasterosteiformes

Hypoptychidae (Fig. 11). The palatine is edentulous and bears a laterally projected cylindrical head. The ectopterygoid is elongated and posteriorly expanded into a triangle that lies on the lateral surface of the quadrate and extends to the metapterygoid. The endopterygoid is absent. Orr (1995) identified an endopterygoid in Hypoptychidae, but I argue that what he identified as an endopterygoid is the lateral ethmoid. The metapterygoid is reduced to a small splint over the symplectic. The quadrate is fanlike and bears a distinct ventral process. The symplectic is rod-like and not fully inserted in the quadrate. The hyomandibular bears distinct dorsal condyles, but lacks the lateral lamina and anterior flange.

The preopercle is smooth, with a distinct ventral arm, and bears a preoperculomandibular canal. The interopercle is long and broader posteriorly. The subopercle bears a small ascending process and its posterior margin is pointed. The opercle lacks an anterior strut. Also see Ida (1976).

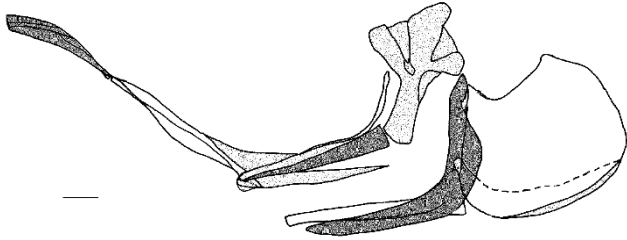


Fig. 11. Lateral view of the suspensorium and opercular series in *Hypoptychus dybowskii* (Hypoptychidae) (UAMZ 5550, 80 mm).

Aulorhynchidae (Fig. 12). The palatine is edentulous and bears a straight conical head. The ectopterygoid is T-shaped with a long posterior arm and short anterior and ventral arms and posteriorly articulated with the symplectic. The endopterygoid is absent. The metapterygoid is reduced. The quadrate is fanlike and bears a highly elongated ventral process. The symplectic is cylindrical and with a bifurcated dorsal flange. The hyomandibular bears distinct dorsal condyles in *Aulorhynchus* (not distinct in *Aulichthys*) and a small lateral lamina.

The preopercle is smooth, with an elongated ventral arm, and bears a preoperculomandibular canal. The interopercle is elongated and broader posteriorly. The subopercle bears a distinct ascending process and its posterior margin is fimbriated. The opercle lacks an anterior strut.

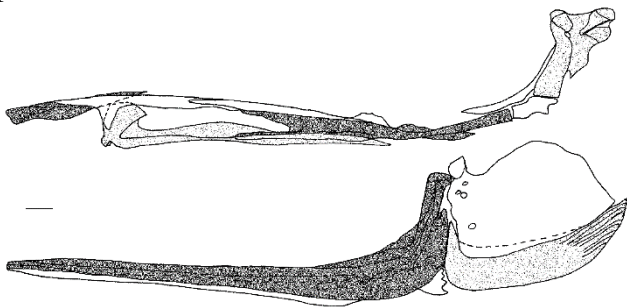


Fig. 12. Lateral view of the suspensorium and opercular series in *Aulorhynchus flavidus* (Aulorhynchidae) (UAMZ 3783, 109 mm).

Gasterosteidae (Fig. 13). The palatine is edentulous and bears a straight conical head. The ectopterygoid and endopterygoid are fused into a triradiate bone which embraces the anterior and dorsal margins of the quadrate. The metapterygoid is reduced. The quadrate is fanlike and bears a distinct ventral process. The symplectic is cylindrical and with bifurcated dorsal and ventral flanges. The hyomandibular bears distinct dorsal condyles, a small lateral lamina, and an anterior flange.

The preopercle is smooth, with an elongated ventral arm, and bears a preoperculomandibular canal. The interopercle is broader posteriorly. The subopercle bears a well-developed ascending process and its posterior margin is fimbriated. The opercle is roughly triangular and lacks an anterior strut. Also see Keivany (1996, 2000), Keivany et al. (1997) and Keivany & Nelson (1998, 2000, 2004, 2006).

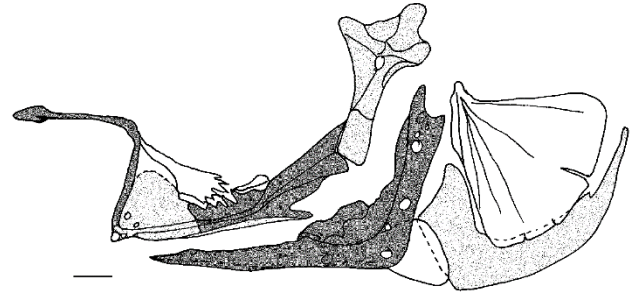


Fig. 13. Lateral view of the suspensorium and opercular series in *Pungitius pungitius* (Gasterosteidae) (UAMZ 3049, 46 mm).

Pegasidae. The palatine, ectopterygoid, endopterygoid, and metapterygoid are absent. Bowne (1985, 1994) believed that the maxillovomerine ligament of Pietsch (1978) was the palatine and Jungerson (1915) argued that it was the fused palatine and ectopterygoid without giving evidence for compound origins (though It was observed two centers of ossification in the specimens; one anterior and the other posterior). Orr (1995) followed Pietsch (1978) and these structures might not be homologous with the palatine and ectopterygoid. The quadrate is small and bears an expanded ventral process. The symplectic is cylindrical and bears a bifurcated dorsal flange and a ventral flange. The hyomandibular bears

separate dorsal condyles and the posterior one is elongated. A large medial lamina reduces movement of the suspensorium.

The preopercle is toothed, without a distinct ventral arm, but highly enlarged, approaching its counterpart ventrally covering most of the ventral surface of the head, and bears a preoperculomandibular canal and a socket at its articulation with the interhyal. The interopercle is elongated and widely separated from the subopercle and opercle. The subopercle is reduced and bears a distinct ascending process. The opercle is also highly reduced and lacks struts.

Solenostomidae (Fig. 14). The palatine is edentulous, fused to the vomer and bears a laterally projected cylindrical head. The ectopterygoid is curved. The endopterygoid is narrow and elongated at the quadrate dorsal margin. The metapterygoid is fused to the symplectic in adults. The quadrate is fan-like and bears a long ventral process with a broad dorsal flange. The symplectic is cylindrical and with a ventral flange. The hyomandibular bears distinct dorsal condyles and a small lateral lamina. A large medial lamina reduces movement of the suspensorium.

The preopercle bears several small lateral spines, a long posteroventral spine, an elongated ventral arm, and a preoperculomandibular canal. The interopercle is elongated and widely separated from the subopercle and opercle. The subopercle is thread-like, curved around the opercle, and lacks a distinct ascending process. The opercle is concave and bears spiny anterior and dorsal struts. As Orr (1995) noted, the interhyal lamina is attached to the posteroventral corner of the preopercle.

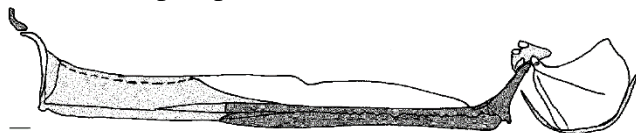


Fig.14. Lateral view of the suspensorium and opercular series in *Solenostomus paradoxus* (Solenostomidae) (AMS 17111002, 51 mm).

Syngnathidae (Fig. 15). The palatine is edentulous and bears a bud-like head. The ectopterygoid is thin and curved at the anterior margin of the quadrate. The endopterygoid is narrow at the quadrate dorsal edge. The metapterygoid is fused to the symplectic in adults, but autogenous in young (Azzarello 1989). The quadrate is fan-like and bears a long ventral process with a broad dorsal flange. The symplectic is cylindrical and with a ventral flange. The hyomandibular bears distinct dorsal condyles, a lateral lamina, and an anterior flange. A large medial lamina restricts movement of the suspensorium.

The preopercle bears a strong posteroventral process, an elongated, angled ventral arm, a preoperculomandibular canal, and a socket at its articulation with the interhyal. The interopercle is elongated and widely separated from the subopercle and opercle. The subopercle is thin, curved, mostly overlaps the opercle, and lacks a distinct ascending process. The opercle is concave and lacks the struts. The gill opening is reduced to a small pore on the top of the opercle.

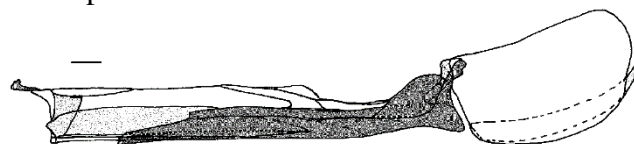


Fig.15. Lateral view of the suspensorium and opercular series in *Syngnathus scovelli* (Syngnathidae) (UAMZ 3782, 117 mm).

Indostomidae (Fig. 16). There are no distinct palatine, ectopterygoid and endopterygoid bones. Instead, there is a single long bone that connects the quadrate to the ethmoid region and might be homologs of the palatine, ectopterygoid and endopterygoid bones (Banister, 1970). The metapterygoid is small and located dorsal to the symplectic-hyomandibular complex. The quadrate is without a distinct ventral process. The symplectic is simple and without the flanges. The hyomandibular bears distinct dorsal condyles.

The preopercle is triangular and lacks a ventral arm. The interopercle is absent, as noted by Johnson

and Patterson (1993) and Orr (1995). The subopercle is a thread-like bone inside the opercle and does not bear an ascending process. The opercle is concave, bears six conspicuous posterior spines, and lacks struts.

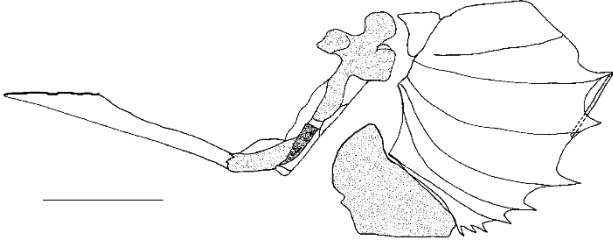


Fig.16. Lateral view of the suspensorium and opercular series in *Indostomus paradoxus* (Indostomidae) (CAS 64017, 25 mm).

Aulostomidae (Fig. 17). The palatine is short and edentulous. The ectopterygoid is thin, T-shaped with a long posterodorsal arm and a short ventral arm at the anterior margin of the quadrate. The endopterygoid is absent. The metapterygoid is independent in juveniles, but fused to the symplectic in adults (Azzarello 1989). The quadrate is fanlike and bears a long ventral process with a broad dorsal flange. The symplectic is cylindrical and with a dorsal flange. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina.

The preopercle bears an elongated ventral arm, and bears a preoperculomandibular canal. The interopercle is elongated and slightly broader posteriorly. The subopercle is thin, fimbriated posteriorly, and bears an enlarged triangular ascending process. The opercle is fimbriated posteriorly and lacks struts.

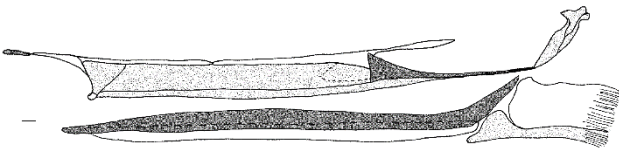


Fig.17. Lateral view of the suspensorium and opercular series in *Aulostomus valentini* (Aulostomidae) (CAS 11979, 139 mm).

Fistulariidae. The palatine is short, edentulous and bears a laterally projected head. The ectopterygoid is thin, and T-shaped with a long posterodorsal arm and

a short ventral arm at the anterior margin of the quadrate. The endopterygoid is elongated and its dorsal edge is spinous. The metapterygoid is fused to the symplectic in adults. The quadrate is fanlike and bears a long ventral process with a broad dorsal flange. The symplectic is cylindrical and with well-developed flanges. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina.

The preopercle bears an elongated ventral arm and a preoperculomandibular canal. The interopercle is elongated extending along the opercle. The subopercle bears an enlarged triangular ascending process. The opercle is fimbriated posteriorly and lacks struts.

Macroramphosidae (Fig. 18). The palatine is edentulous and bears a small laterally projected head with a tiny posteromedial process. The ectopterygoid is curved. The endopterygoid is elongated. The metapterygoid is triangular. The quadrate is fan-like and bears a long ventral process with a broad dorsal flange. The symplectic bears developed flanges. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina. A large medial lamina restricts movement of the suspensorium.

The preopercle bears an elongated ventral arm, a posteroventral process, a preoperculomandibular canal, and a socket at its articulation with the interhyal. The interopercle is elongated and slightly broader posteriorly. The subopercle bears a distinct ascending process. The opercle bears an anterior strut.

Centriscidae. The palatine is small, edentulous, and bears no distinct head but a tiny posteromedial process. The ectopterygoid is small and triangular. The endopterygoid is elongated. The metapterygoid is thin and triangular. The quadrate is fan-like and bears a long ventral process with a broad dorsal flange. The symplectic bears a developed flanges. The hyomandibular is pointed and lacks distinct dorsal condyles. A large medial lamina restricts movement of the suspensorium.

The preopercle bears an elongated ventral arm, a large posteroventral process, a

preoperculomandibular canal, and a socket at its articulation with the interhyal. The interopercle is elongated and slightly broader anteriorly and widely separated from the subopercle. The subopercle bears a large ascending process. The opercle bears no struts. Also see Mohr (1937).

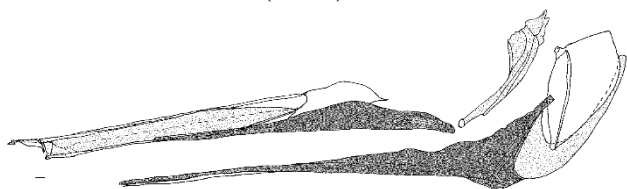


Fig.18. Lateral view of the suspensorium and opercular series in *Macroramphosus scolopax* (Macroramphosidae) (USNM 344398, 99 mm).

Synbranchiformes

Synbranchidae (Fig. 19). The palatine is small, toothed, and without a head, but with a small lateral process. The ectopterygoid is toothed and enlarged. The endopterygoid is fused to the dorsolateral margin of the ectopterygoid. The metapterygoid is fan-like, broad and lies posterior to the quadrate. The quadrate is fanlike and has a distinct ventral process. The symplectic is rod-like. The hyomandibular is short and lacks distinct condyles.

The preopercle lacks a distinct ventral arm, evenly broad, obliquely positioned, and bears a preoperculomandibular canal. The interopercle is broad and widely separated from other elements of opercular series. The subopercle bears a triangular ascending process and is fimbriated posteriorly. The opercle lacks the struts and is fimbriated posteriorly.

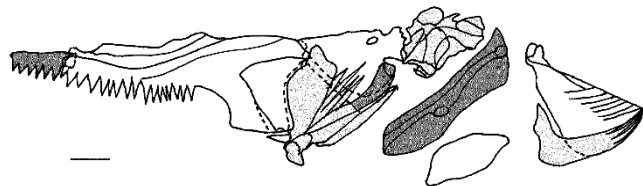


Fig.19. Lateral view of the suspensorium and opercular series in *Monopterus albus* (Synbranchidae) (USNM 192939, 193 mm).

Mastacembelidae. The palatine is long, edentulous, and without a distinct head. The ectopterygoid is broad. The endopterygoid is narrow and autogenous

at the dorsomedial margin of the ectopterygoid. The metapterygoid is fan-like, broad, and lies posterior to the quadrate. The quadrate is fan-like and with a distinct ventral process. The symplectic is rod-like, long, and has small dorsal and ventral flanges. The hyomandibular is short, bears distinct anterodorsal and posterodorsal condyles, a lateral lamina, and a small anterior flange.

The preopercle bears a ventral arm and a preoperculomandibular canal. The interopercle is long and broader posteriorly. The subopercle bears a triangular ascending process and is fimbriated posteriorly. The opercle lacks the struts and is fimbriated posteriorly. Also see Rosen & Greenwood (1976) and Travers (1984).

Scorpaeniformes

Dactylopteridae (Fig. 20). The palatine is edentulous, fused to the ectopterygoid, and has a cylindrical head that bears a small lateral process. The ectopterygoid is large. The endopterygoid lies on the medial faces of the ectopterygoid. The metapterygoid is autogenous. The quadrate is fan-like and has a distinct ventral process. The symplectic lies perpendicular to the quadrate. The hyomandibular bears distinct dorsal condyles and well-developed lateral and medial laminae.

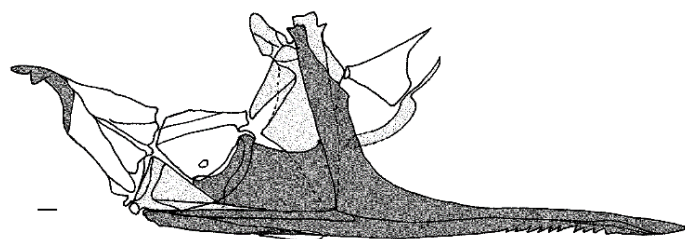


Fig.20. Lateral view of the suspensorium and opercular series in *Dactylopterus volitans* (Dactylopteridae) (UAMZ 2633, 74 mm).

The preopercle bears a distinct ventral arm, a long toothed posteroventral process, an anterior flange, and a preoperculomandibular canal. The interopercle is small and widely separated from the subopercle. The subopercle is highly reduced and has a long

posterior process, but no ascending process. The opercle is also reduced and lacks struts. Also see Doyle (1998).

Scorpaenidae. The palatine is long, toothed, and with a laterally projected cylindrical head. The ectopterygoid is L-shaped. The endopterygoid is broad and autogenous at the dorsomedial margin of the ectopterygoid. The metapterygoid is autogenous, fan-like, and lies posterior to the quadrate. The quadrate is fan-like and with a distinct ventral process. The symplectic is rod-like. The hyomandibular bears a large head without distinct condyles, but bears a small lateral lamina and an anterior flange.

The preopercle possesses a ventral arm and a preoperculomandibular canal. The interopercle is broad and situated below the preopercle and overlaps the preopercular spines. The subopercle bears a distinct ascending process and a long posterior process. The opercle bears the anterior and dorsal struts and three posterior spines.

Hexagrammidae (Fig. 21). The palatine is edentulous and has a laterally projected cylindrical head. The ectopterygoid is T-shaped. The endopterygoid is narrow and autogenous, lying at the dorsomedial margin of the ectopterygoid. The metapterygoid is autogenous, fan-like, and lies posterior to the quadrate. The quadrate is also fan-like with a distinct ventral process. The symplectic is rod-like. The hyomandibular bears a large head without distinct condyles, but bears a small lateral lamina and an anterior flange. The palatine is toothed in some specimens of *Hexagrammos*, *Oxylebius*, *Zaniolepis*, and *Ophiodon* (Shinohara 1994).

The preopercle bears a ventral arm, a preoperculomandibular canal, and four lateral arches. The interopercle is broad situating below the preopercle. The subopercle bears distinct ascending and posterior processes. The opercle lacks struts.

Agonidae (Fig. 22). The palatine is long, toothed, and with a cylindrical head. The ectopterygoid is curved. The endopterygoid is autogenous and reduced to a small splint. The metapterygoid is

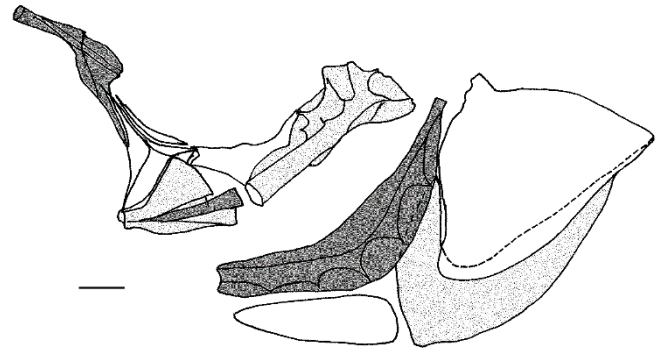


Fig.21. 21. Lateral view of the suspensorium and opercular series in *Hexagrammmus decagrammus* (Hexagrammidae) (UAMZ 3190, 50 mm).

autogenous, fan-like, and lies posterior to the quadrate. The quadrate is fan-like and with a distinct ventral process. The symplectic is rod-like. The hyomandibular bears no distinct condyles, but bears a small lateral lamina and an anterior flange. In some genera (e.g., *Percis*, *Agnus*, and *Bathyagonus*), the palatine is edentulous and in *Hypsagonus*, the endopterygoid is relatively large (Kanayama 1991).

The preopercle bears a ventral arm, a preoperculomandibular canal, and five large lateral arches. The interopercle is long and broader posteriorly. The subopercle bears a distinct ascending and a long posterior process. The opercle is triangular and bears the anterior and dorsal struts and three posterior spines.

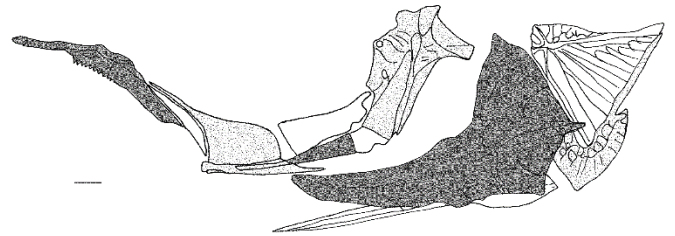


Fig.22. Lateral view of the suspensorium and opercular series in *Xeneretmus latifrons* (Agonidae) (UAMZ 3196, 95 mm).

Perciformes

Percidae. The palatine is short, toothed, with a laterally projected head, and lies ventral to the ectopterygoid. The ectopterygoid is triradiate and autogenous. The endopterygoid is broad and connected to the medial face of the ectopterygoid. The metapterygoid is broad and autogenous. The quadrate is fan-like and with a distinct ventral

process. The symplectic is rod-like. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange.

The preopercle is toothed and has a broad ventral arm and a preoperculomandibular canal. The interopercle is broad. The subopercle bears a small ascending process. The opercle bears a dorsal strut.

Cirrhitidae. The palatine is short, with a few small teeth and a laterally projected head, and lies ventral to the ectopterygoid. The ectopterygoid is triradiate and autogenous. The endopterygoid is broad and connected to the medial surface of the ectopterygoid. The metapterygoid is broad and autogenous. The quadrate is fan-like, with a distinct ventral process. The symplectic is rod-like. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange.

The preopercle is toothed, with a broad ventral arm, and a preoperculomandibular canal. The interopercle is broad. The subopercle bears a small ascending process and is fimbriated posteriorly. The opercle bears a dorsal strut.

Elassomatidae (Fig. 23). The palatine is edentulous and has a laterally projected head. The ectopterygoid and endopterygoid are absent. The metapterygoid is relatively broad and autogenous. The quadrate is fanlike and with a distinct narrow ventral process. The symplectic is rod-like. The hyomandibular bears a distinct posterodorsal condyle, a small lateral lamina, and an anterior flange.

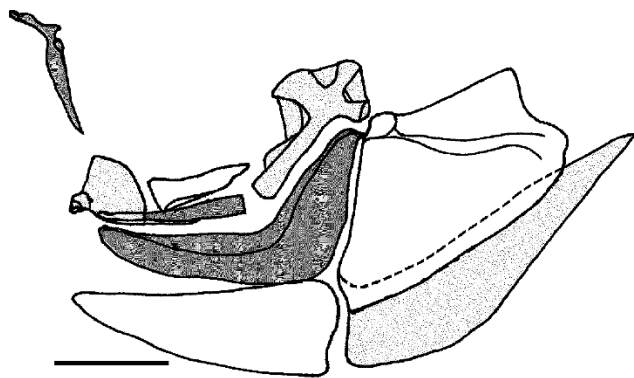


Fig.23. Lateral view of the suspensorium and opercular series in *Elassoma zonatum* (Elassomatidae) (UAMZ 6920, 30 mm).

The preopercle is smooth and with a distinct ventral arm and a preoperculomandibular canal. The interopercle is triangular. The subopercle bears a small ascending process. The opercle bears a dorsal strut. Also see Johnson & Spriner (1997) and Jones & Quattrro (1999).

Pomacentridae. The palatine is short, edentulous, with a laterally projected head, and lies on the lateral surface of the ectopterygoid. The ectopterygoid is triradiate, and tightly attached to the quadrate. The endopterygoid is broad and fused to the medial surfaces of the ectopterygoid and quadrate. The metapterygoid is broad and fused to the symplectic-hyomandibular. The quadrate is fan-like and its ventral process is confluent with the quadrate body. The symplectic is rod-like. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange. There is a tendency in most of the elements to fuse together.

The preopercle is toothed, with a broad ventral arm, and a preoperculomandibular canal. The interopercle is broad. The subopercle bears a small ascending process. The opercle bears the anterior and dorsal struts.

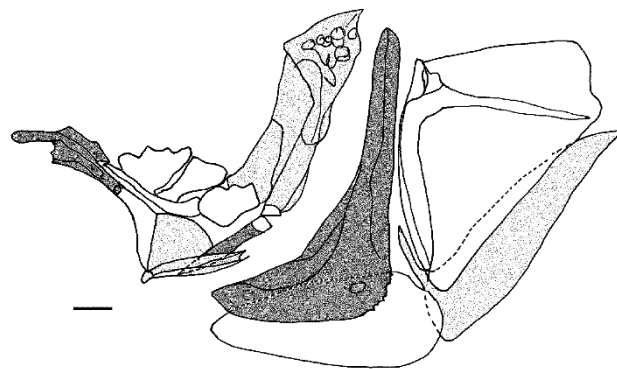


Fig.24. Lateral view of the suspensorium and opercular series in *Lepomis gibbosus* (Centrarchidae) (UAMZ 7715.4, 40 mm).

Centrarchidae (Fig. 24). The palatine is edentulous, with a laterally projected head, and lies on the lateral surface of the ectopterygoid. The ectopterygoid is curved and tightly attached to the quadrate. The endopterygoid is broad. The metapterygoid is broad and connected to the quadrate. The quadrate is fan-

like and without a distinct ventral process. The symplectic is rod-like. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange.

The preopercle is smooth, with a broad ventral arm and a preoperculomandibular canal. The interopercle is broad. The subopercle bears a small ascending process. The opercle bears an anterior and a dorsal strut.

Acknowledgements

I would like to express my gratitude to late Professor J.S. Nelson, Dr. P.R. Willoughby, Dr. M.V.H. Wilson, Dr. B.S. Heming, Dr. G. Goss and Dr. L.R. Parenti for providing helpful comments and advice during the course of this study. I wish to extend my sincere appreciation to Mr. W.E. Roberts for lending museum materials and Mr. R. Mandryk for preparing stains and other chemical solutions, the curators and staff of the Smithsonian Institution, California Academy of Sciences, and Australian Museum at Sydney for lending their fish specimens. This study was financially supported by a MCHE scholarship to the author, a NSERC grant to Professor J.S. Nelson and Isfahan University of Technology.

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